

A SHORT NOTE ON SEED PREDATION IN *WATSONIA PYRAMIDATA* (ANDR.) STAPF IN RELATION TO SEASON OF BURN

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ABSTRACT

Watsonia pyramidata is a common geophyte in the south western Cape, where it is well known for its spectacular mass flowering following summer and autumn fires. The results of a small field trial suggest that this synchronous flowering serves to minimise pre- and post-dispersal seed predation. The remaining seed can then germinate and the seedlings can establish themselves in the favourable post-fire environment. Seedling regeneration is absent between fires and following fires between April and October and sexual reproduction is therefore limited to the occurrence of summer and autumn burns.

'N KORT NOTA OOR DIE VREET VAN *WATSONIA PYRAMIDATA* (ANDR.) STAPF SAAD IN VERHOUDING TOT DIE BRANDTYD

Watsonia pyramidata is 'n geofiet wat volop in die Suidwes-Kaap voorkom waar dit goed-bekend is vir die aanskoulike massavertoning blomme na somer- en herfsveldbrande. Die resultate van 'n klein veld-proefneming suggereer dat die gelyktydige blom van al die plante dien om die verlies aan saad voor en na verspreiding, te verminder. Die oorblywende saad ontkiem dan en die saailinge word gevestig in die gunstige na-brandse omgewing. Saailingregenerasie is afwesig tussen brande en ook na brande tussen April en Oktober en dus is seksuele voortplanting beperk tot die voorkoms van somer-en herfsbrande.

Key words: *Watsonia pyramidata*, seed predation, fire, seedling regeneration.

INTRODUCTION

Fire is a major ecological factor controlling the development of the sclerophyll vegetation (fynbos) of the mediterranean regions of the world (Specht, 1979). The regeneration from seed of the fynbos plants appears to be almost entirely restricted to the first year following a fire, and is influenced by season of burn. *Watsonia pyramidata* (Andr.) Stapf (Iridaceae) is an example of a species with a marked response to season of burn. *W. pyramidata* is a typical mountain fynbos geophyte and is widely distributed in the mountain ranges of the south western Cape where it generally occurs in dense populations. The tough sclerophyllous leaves reach 1.0 m in

length and the inflorescences attain 1,4 m in height. It has long-lived clones made up of one to many ramets, each with its own corm (Kruger, 1978). In non-flowering years a new corm develops from the apical bud and replaces the previous one, but when the ramet flowers two new corms are formed from axillary buds as the apical bud which elongated to form the inflorescence dies. The two new corms give rise to two ramets in place of the original ramet. In normal years less than 10% of the ramets flower but when the population is subjected to a late summer or autumn burn, mass flowering is induced in the succeeding spring. The exact nature of the stimulus is uncertain but it may be related to heating of the corms during the fire, nutrients released by the fire (Bean, 1962), increased light, increased soil moisture or any combination of the above factors.

The phenomenon of mass flowering is in many ways comparable to the mast fruiting of certain tropical trees. Waller (1979) has examined the relationship between mast fruiting and life history parameters of these trees and concluded that they should have high adult survivorship and low population growth. Janzen (in Waller, 1979) concluded that high seed predation favours this form of reproduction. This mass flowering, fruiting and seed shed overwhelms the seed predators and allows sufficient seed to set and germinate and also reduces seedling mortality during establishment (Chan, 1980).

This study was designed to test the hypothesis that mass flowering and the consequent seed set and shed in *Watsonia pyramidata*, following burns in the "natural" fire season (summer to autumn) result in predator satiation and ensure an adequate seed pool for germination and population expansion. *W. pyramidata*'s population dynamics are being studied in ongoing work at Jonkershoek. This study was designed to supplement the ongoing studies and sought to answer the following questions:

- (1) What levels of seed predation are found:
 - (a) in the first season following:
 - (i) spring (poor flowering) burns;
 - (ii) late summer to autumn (mass flowering) burns;
 - (b) in populations in their second flowering season?
- (2) What types of granivores are involved?

METHODS

The sites selected for this experiment (see Fig. 1) all lie within the Jonkershoek Valley. Two broad parallel firebreaks, burnt approximately every six years, cross the valley at right angles. One half of each has a northerly aspect and the other a southerly aspect. Three study sites were placed

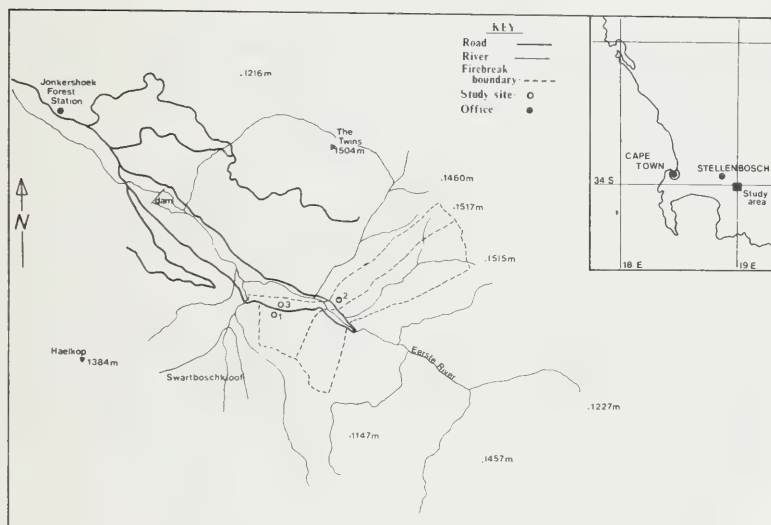


FIG. 1.

A map showing the locality of the study site, the main features of the area, the autumn burn (Site 1), the older vegetation (Site 3) and the spring burn (Site 2) study areas.

within these two breaks, but in areas burnt at different times. These are designated the autumn burnt (site 1), spring burnt (site 2) and older sites (site 3) (see Table 1). The community is dominated by restioid and graminoid components with a number of small shrubs and taller resprouting shrubs (Van Wilgen, 1980). Salient features of the sites are given in Table 1.

Seed fall was measured by trapping the falling seed and this was checked against an estimate of the seed produced by the population. Post-dispersal predation was estimated by means of selective predator exclusion. Seed release in *W. pyramidata* occurs during January and February (Kruger, 1988) and the experiment was timed to coincide with the first seed fall following the autumn burn at site one.

The seed traps were constructed of 50×12 mm wood to give an internal area of 250×250 mm. Masonite 4 mm thick was used for the base and the top was covered with 12 mm diamond mesh to exclude small mammals and birds. Small rodents such as *Mus minutoides* can penetrate this mesh but the length (6–8 mm) and the low mass (0.016 g) of *W. pyramidata* seed pre-

TABLE 1.
Details of the three study sites selected for this experiment

Details/Site	1	2	3
Aspect	North east	South east	North
Slope	10 deg.	5 deg.	6 deg.
Soil	Loam, derived from Table Mtn. Sandstone and Granite	As for site 1	As for site 1
Date of last burn	30 April 1980	21 October 1980	September 1980
Season of last burn	Autumn	Spring	Spring
Flowering season	First	First	Second

cluded any smaller mesh. Half of these traps were dipped in *Chlorpirifos* (a class B2 organo-phosphate poison) to exclude insects.

Two 50-m long parallel lines—each with trap stations at 5 m intervals—were laid out at site one on 12 January 1981. At each of the trap stations on each line a pair of traps, one poisoned and one unpoisoned, was placed and a section of soil $250 \times 250 \times 20$ mm deep was removed, and sieved for seed. This seed was counted and removed, and the soil replaced and tamped down. By this means a comparison between unhindered predation, predation primarily by insects, and no predation could be made.

At this site the population density of *W. pyramidata* and the proportion of the ramets in flower was estimated by means of a wandering quarter (Catana, 1963) survey on 16 January 1981. Sample inflorescences were collected on the same day to estimate the potential seed fall, for comparison with the seed densities estimated from the trap counts.

On 12 March 1981 at sites two and three, 10 batches of 10 seeds each were placed on the soil at 5-m intervals along a line chosen so that it passed through a *W. pyramidata* population. The number of seed at each point were counted at the subsequent surveys in order to obtain an estimate of seed predation rates on those sites relative to the autumn burnt site.

Pre-dispersal predation was estimated by counts of the numbers of whole and bored or gnawed ovaries per inflorescence. A wandering quarter sample was used to select random inflorescences at site one. The pre-dispersal predation at sites two and three was assessed by counting ovaries on the first ten available inflorescences as there were too few for a random selection.

TABLE 2.

Numbers of seed counted at site 1 at establishment and during the two subsequent visits. The seed sieved from the soil sample was counted and removed. The number of seed counted on 10 March is the total for the period 12 January to 10 March as no seed was removed on 23 January

Station	Date and purpose of the Visit					
	Establishment 12 Jan. 1981	Check Count 23 Jan. 1981		Termination 10 March 1981		
	Seed in soil	seed in traps		seed in traps		Soil
		pois.	unpois.	pois.	unpois.	
1	0	5	1	8	3	3
2	3	13	5	26	17	3
3	9	6	6	10	10	2
4	23	5	3	9	7	1
5	1	5	1	8	0	1
6	0	19	10	19	12	2
7	4	2	1	5	6	0
8	9	2	2	9	5	8
9	17	4	6	15	13	11
10	12	4	3	16	7	9
11	31	1	0	15	8	3
12	2	7	8	16	14	12
13	13	4	1	5	1	9
14	0	0	1	0	2	0
15	8	8	0	7	2	10
16	10	0	0	1	0	3
17	7	1	0	1	0	0
18	4	5	3	4	2	0
19	10	1	0	0	0	1
20	4	7	4	11	7	4
Mean	8.35	4.85	2.75	9.25	5.85	4.10

RESULTS

Watsonia pyramidata had started shedding its seed before this study was initiated on 12 January 1981. This was the source of the seed found in or on the soil on 12 January (see Table 2). Seed shed continued until early March, a period of 8 or 9 weeks. Inspection of the inflorescences showed that seed shed, like bud development and flowering, followed an acropetal pattern and probably took about two weeks per inflorescence.

At site one the wandering quarter density calculations give a density of

TABLE 3.

Numbers of ovaries per inflorescence and the percentage bored or partly eaten by insects at three sites. This count was done on 12th March 1981

Inflorescence No.	Site No. 1		Site No. 2		Site No. 3	
	No. of ovaries	% bored	No. of ovaries	% bored	No. of ovaries	% bored
1	19	0,0	26	0,0	25	32,0
2	11	9,1	14	35,7	36	36,1
3	16	0,0	20	10,0	32	78,1
4	27	3,7	27	40,7	17	52,9
5	24	12,5	24	37,5	2	50,0
6	35	0,0	31	38,7	23	60,9
7	19	0,0	18	33,3	18	0,0
8	19	5,3	9	22,2	15	0,0
9	18	5,6	12	25,0	21	57,1
10	26	0,0	18	27,8	19	21,1
Mean	21,4	3,62	19,9	27,1	20,8	38,8

2,15 (Std. Dev. = 0,11; Ashton, 1976) ramets per square metre or about 1,38 clones per square metre. Of these ramets 55,71% had flowered. Fifteen inflorescences randomly collected were used to estimate the mean number of full, undamaged seed per ramet, which was 220,40 (Std. Dev. = 92,03) or about 264 (Std. Dev. = 110) seed per m². This estimate is not significantly different from the estimate of total seed fall obtained as the sum of the mean number of seed removed from the soil on 12 January 1981 and the mean number of seed in the poisoned traps, which is 281,60 (Std. Dev. = 176,53) seed per m². If all this seed had germinated there would have been a more than 100-fold increase in the population size.

The wandering quarter survey shows that *W. pyramidata* occurs in clumps that are not randomly distributed. This, the skew distribution of seed densities in the seed traps, and the low sample size, suggested the use of a non-parametric Mann-Whitney test (Zar, 1974, p.108) rather than a t-test or multiple range tests. This test shows that the seed densities found on 10 March 1981 differ markedly (2 % level of significance) for the poisoned traps vs the soil samples, but only at the 20 % level for the poisoned vs unpoisoned and unpoisoned vs soil sample densities.

By 12 March 1981 seed shed was complete at site one, but there was abundant seed still lying on the soil surface. By 24 April 1981—when the last count was made at site three—there was very little seed still evident on the

TABLE 4

Seed predation at the spring burnt sites in the first and second flowering season. Ten seeds were placed at each station on 12 March 1981, and the numbers were re-counted on the dates given below

Station	Site 3: Second Season			Site 2: First Season	
	20 March	27 March	24 April	20 March	27 March
1	10	10	8	5	0
2	10	10	6	9	0
3	10	10	6	3	0
4	10	8	6	0	0
5	10	9	9	0	0
6	10	9	1	4	0
7	10	7	7	0	0
8	10	9	2	7	0
9	10	9	8	6	0
10	10	9	7	3	0
Mean	10,00	9,00	6,00	3,70	0,00

soil surface at site one. No seed was observed lying on the soil surface at either of the other two sites, probably as a result of the pre- and post-dispersal predation and the low proportion of plants in flower ($< 10\%$). Results are summarised in Tables 2 to 4.

The same test applied to the pre-dispersal predation shows that the predation was much less at site one than at sites two and three (0,5 % and 1 % level of significance respectively). The latter two sites are not statistically different in pre-dispersal predation rates although the rates of "post-dispersal" predation are significantly different (0,1 % level of significance).

DISCUSSIONS AND CONCLUSIONS

The satiation hypothesis rests primarily on the assumption that the large fruit and seed crop produced periodically provides sufficient excess to allow the establishment of seedlings despite a possible increase in pre- and post-dispersal predation. If therefore sampling of vegetation with mass and sparsely flowering *W. pyramidata* showed that seedling establishment was equally likely in both cases then the hypothesis would be refuted.

The pre-dispersal predation figures support the satiation hypothesis and suggest that the higher density of the flowers out-weighed the extra attraction of the abundant food source for the primary consumer, a small snout beetle (Circulionidae). Site two has about the same average density of *W.*

pyramidata while site three has a much lower density. After the spring burn on site two less than 10 % of the clones flowered and if this is converted to an area basis it gives about 1,6 bored ovaries per m² on this site against 0,9 for site one.

The post-dispersal predation rates are more difficult to interpret. The differential predator exclosures were successful and worked as expected. The results suggest that insects are more important than birds and rodents in *W. pyramidata* seed predation. This may be because the low aerial plant cover in the young vegetation discouraged rodents (Bond *et al.*, 1980), although this scarcely affects nocturnal species (J. Breytenbach, W. Bond, pers. comms.).

This factor may also account for the lower seed predation rates at site three in relation to the spring burn site two as the vegetation on site three is more open. A further factor that could reduce rodent populations is the fact that on all these sites the post-fire seed store would have been depleted (J. Breytenbach, pers. comm.). At the end of the season the visible seed had apparently been removed on all sites. A count of seedling densities in November 1982 gave a seedling density of two to three per square metre on site one, but none could be found at sites two or three. The seedling density could be higher as they are difficult to spot except in open areas. Kruger (1978) found initial seedling densities as high as 75 times the parent population, but the seed to seedling ratio in his study (ca. 4, 5) is about the same as that on site one (ca. 5,0).

The hypothesis that this mass flowering response is a means of establishing seedlings in an environment with the maximum availability of suitable sites for its particular regeneration niche can be seen as an extension of the primary hypothesis. Seedling establishment is an extremely vulnerable stage in the life-cycle of a plant (Harper, 1977) and the requirements of the regeneration niche (Grubb, 1977) are critical at this stage. The primary hypothesis states that this mass flowering is a means of producing a maximum seed crop to fill the available regeneration niches and thus meets the requirements of this second hypothesis. Neither hypothesis however, suggests why this response is linked to season of burn because seed regeneration seems to be primarily restricted to the wet season (le Maitre, in prep.; Wicht, 1948) and because *W. pyramidata*'s flowering season is not altered by season of burn. This means that the availability of regeneration niches would probably be the same regardless of season of burn, and that a mass flowering response should give much the same population increase regardless of season of burn. The response to burning during the "natural" fire season must therefore be linked to the phenology of *W. pyramidata*, but this postulate could not be tested during this experiment.

One major question which should be tackled in any future studies that

are designed to substantiate the satiation hypothesis, and the results of this experiment, is the problem of the fate of the majority of the seed. The mass flowering response does enable the species to establish large seedling populations in years following burns in the "natural" fire season. This is important for the long term conservation of the species because it enables the species to reproduce sexually and maintain its genetic diversity as well as maximising its vegetative reproduction.

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